Spatial and Temporal Dynamics of Overwintering *Homalodisca coagulata* (Hemiptera: Cicadellidae)

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ABSTRACT A 4-yr landscape-scale study was conducted to investigate spatial and temporal dynamics of overwintering *Homalodisca coagulata* (Say) (Hemiptera: Cicadellidae) in the lower San Joaquin Valley, California. Spatial structures of *H. coagulata* distributions were characterized with Moran's *I* index, and spatial associations between *H. coagulata* and the surrounding environment were investigated with a geographic information system. *H. coagulata* was caught consistently with sticky traps throughout the winter, and trap catches formed a distinctive peak in December or January, indicating active flight of *H. coagulata* during the winter. In 2000–2001, the mean ± SE trap count was 4.8 ± 1.21 per trap per wk, and *H. coagulata* trap catches were spatially autocorrelated within ≈1.3 km. Approximately 49% of *H. coagulata* were caught in citrus, 23% in stone fruit, and 11% in grape. After a control program began in spring 2001, the mean trap count was considerably lower (0.041 ± 0.0004 per trap per wk), and no spatial autocorrelations were detected in 2001–2004. *H. coagulata* trap catch–crop associations also changed after initiation of the control program. Between 25 and 38% of *H. coagulata* trap catches were from citrus, between 8 and 20% were from stone fruit, and between 11 and 25% were from grape. Potential for winter-season spread and management of *Xylella fastidiosa* Wells et al., a pathogen causing Pierce's disease, are discussed.

KEY WORDS glassy-winged sharpshooter, epidemiology, Moran's *I*, geographic information system

The glassy-winged sharpshooter, *Homalodisca coagulata* (Say) (Hemiptera: Cicadellidae), transmits *Xylella fastidiosa* Wells et al., a xylem-limited bacterium that causes various diseases in agricultural and ornamental plants (Blua et al. 1999). One of the most economically important diseases is Pierce's disease (PD) of grapevines, *Vitis vinifera* L. PD has been present in California for >100 yr (Hopkins and Purcell 2002), and infrequent disease epidemics in the north coast region were associated with the sharpshooter *Graphocephala atropunctata* Signoret (Purcell and Frazier 1985). Recent PD epidemics in California have been attributed to *H. coagulata,* a native to the southeastern United States (Sorensen and Gill 1996) that was introduced into California in the early 1990s (Blua et al. 1999). During the past 15 yr, *H. coagulata* has established in many locations throughout California (Purcell and Saunders 1999), including the San Joaquin, Temecula, and Coachella valleys where area-wide insect control programs have been implemented (CDFA 2005, Park et al. 2006a).

Efficient vector insects generally are characterized by a combination of high transmission efficiency, high population density, high propensity for flight, and selection of feeding sites suitable for pathogen transmission (Redak et al. 2004). Although the transmission efficiency of *H. coagulata* is poor compared with other sharpshooters (Turner and Pollard 1959, Almeida and Purcell 2003b), there are several characteristics that make it an effective vector of *X. fastidiosa.* First, *H. coagulata* is considered extremely mobile (Blua et al. 1999) with the capacity to disperse >90 m in a relatively short time (Blackmer et al. 2004). This capacity has enabled it to establish quickly when it is introduced into new geographic areas. Second, *H. coagulata* adults feed on at least 60 plant species and oviposit on at least 48 plant species (Powers 1973, Hoddle et al. 2003), enabling it to use diverse plant landscapes. Third, *X. fastidiosa* also has a wide host range, and *H. coagulata* feeds on some of the same plant species that are common in California. Currently, there are no effective cures for *X. fastidiosa*-infected grapevines (Blua et al. 1999, Blackmer et al. 2004), and growers manage PD by controlling vector insects and by removing diseased vines (Varela et al. 2001). Historically, controlling vector insects had little impact on disease incidence, and removing *X. fastid-*

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iosa-infected vines did not reduce disease spread (Hewitt et al. 1949).

Recent studies by Almeida and Purcell (2003a) and Almeida et al. (2005) showed that overwintering *H. coagulata* can transmit *X. fastidiosa* to dormant grapevine and almond, suggesting potential for PD spread during the winter. Overwintering *H. coagulata* adults potentially carry a high titer of *X. fastidiosa,* because acquisition in late fall occurs when bacterial titers in infected plants are at their highest levels. These large bacterial loads in the foregut of *H. coagulata* combined with feeding during the winter may contribute to PD spread if these inoculations establish chronic infection (Almeida and Purcell 2003a). Feeding on dormant grapevines and almonds also implies that control of *H. coagulata* populations may need to be considered year-round to control PD (Almeida et al. 2005), especially targeting the overwintering population to reduce chronic PD. Although high numbers of overwintering *H. coagulata* have been reported in some areas of California during the past 5 yr (Groves and Chen 2004, Johnson et al. 2004), its overwintering biology is poorly understood. Thus, we analyzed the data from landscape-scale monitoring of *H. coagulata* conducted in four winter seasons in the lower San Joaquin Valley (Kern Co., CA) to investigate the spatial and temporal dynamics of overwintering *H. coagulata.* In this article, the landscape-scale spatial associations of overwintering *H. coagulata* with surrounding commodity types also are reported.

Materials and Methods

***H. coagulata* Monitoring and Georelational Database Construction.** Landscape-scale monitoring was conducted by trapping adult *H. coagulata* during the winter seasons (November–February) of 2000–2004. Trap catches provide a good estimate of *H. coagulata* flight activity. Monitoring areas, covering ≈16,000 ha, were located east of Bakersfield (Kern Co.). During the 2000–2001 winter season, there were 924 trapping locations distributed throughout the area at a distance of ≈160 m (0.1 mile) from each other (Fig. 1). In 2001–2004, 424 trapping locations that were different from 2000 to 2001 trap locations were systematically placed at a distance of ≈400 m (0.25 miles) apart. Each trap was located at least 5 m within a field boundary. At each sample location, a double-sided 17.8- by 22.9-cm yellow sticky trap (Seabright Laboratories, Emeryville, CA) was placed vertically at ≈1.5 m above the ground. Traps were replaced weekly, and the number of *H. coagulata* was counted. These traps were part of an areawide *H. coagulata* management program by the California Department of Food and Agriculture, and current map data can be assessable at http://www.cdfa.ca.gov/phpps/pdcp/gwMaps/gwmaps.htm. All trap locations were georeferenced with a global positioning system and ArcInfo 9 (Environmental Systems Research Institute, Redlands, CA).

Characterization of Spatial Distribution Pattern. The structure of the spatial distribution of *H. coagulata* was investigated by measuring spatial autocorrelation,

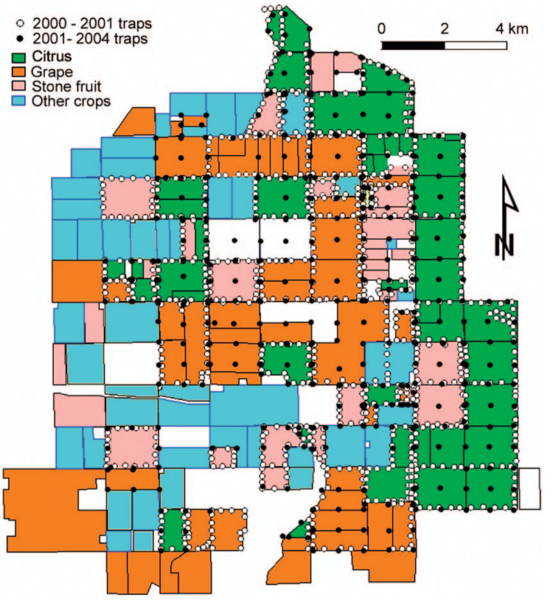

Fig. 1. Agricultural commodities and trap locations in the *H. coagulata* monitoring areas. In 2000–2001 (open circles), there were 924 traps monitored every week, and in the 2001–2004 winters (closed circles), there were 459 traps monitored every week.

an assessment of the correlation of sample values in reference to their locations. Spatial autocorrelation measures the level of spatial dependence between two sample values (Isaaks and Srivastava 1989). Positive spatial autocorrelation occurs when nearby traps have similar values, whereas negative spatial autocorrelation occurs when nearby traps have dissimilar values. Spatial autocorrelation of *H. coagulata* was quantified with Moran's *I* statistics given by

$$I = \frac{N \sum_i \sum_j w_{ij}(x_i - \mu)(x_j - \mu)}{\sum_i \sum_j w_{ij} \sum_i (x_i - \mu)^2}$$

where N is the number of traps; w is a weight factor; x_i and x_j are mean trap catches per week for trap locations i and j, respectively; and μ is the mean of all trap catches. When $I = 0$, there is no spatial autocorrelation (i.e., trap catches are independent of trap location); when $I > 0$, trap catches are more spatially clustered than is expected to occur purely by chance (i.e., traps close to each other tend to have similar trap catches); and when $I < 0$, traps that are closer to each other have dissimilar trap catches, reflecting a lack of clustering. Significance of Moran's *I* was tested using Bonferroni's criterion (Oden 1984). Moran's *I* statistics were calculated with Rooks Case version 0.91 (Laboratory of Paleoclimatology and Climatology, University of Ottawa, Ottawa, Ontario, Canada).

***H. coagulata*–Agricultural Commodity Association.** To investigate the relationship between *H. coagulata* distribution and the surrounding environment, all agricultural commodities in the study area were mapped

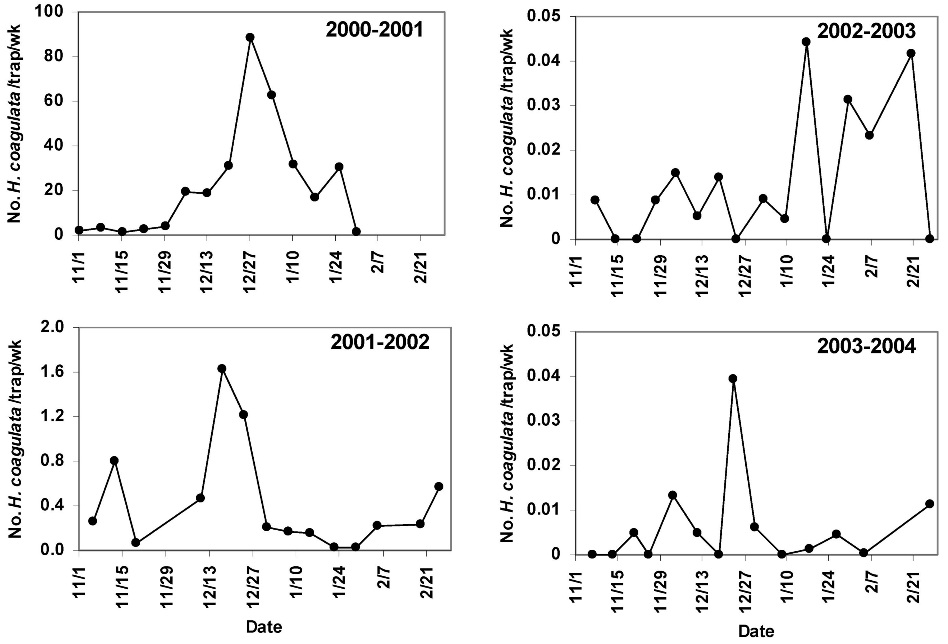

Fig. 2. Temporal dynamics of *H. coagulata* trap catches during the 2000–2004 winter seasons.

with ArcInfo 9 based on 1-m resolution aerial digital imagery photographed in 2002 by the National Aerial Photography Program of the United States of Geological Survey. Digital images were obtained from the Digital Map Library (University of California, Santa Barbara, CA), and commodity information was obtained from the Kern County Agricultural Commissioner's Office (Bakersfield, CA). To determine the spatial relationship of *H. coagulata* with the surrounding environment, total *H. coagulata* trap catches in each commodity type were quantified. The agricultural commodities at each sample location were categorized into four types of vegetation: citrus (orange, lemon, tangerine, grapefruit, and tangelo), grape (raisin, wine, and table grapes), stone fruits (almond, peach, cherry, apricot, and nectarine), and other crops (e.g., alfalfa, blueberry, eucalyptus, pistachio, pomegranate, fig, and orangeberry). The locations of traps and *H. coagulata* catches were compared with the agricultural commodity categories by using Spatial Analyst, an ArcInfo 9 extension (Environmental Systems Research Institute). Trap counts were too low for analyses in most weeks, so trap counts were pooled over weeks in each year for spatial analysis. Because citrus is known as a preferred overwintering and reproductive host for *H. coagulata* (Blua et al. 1999,

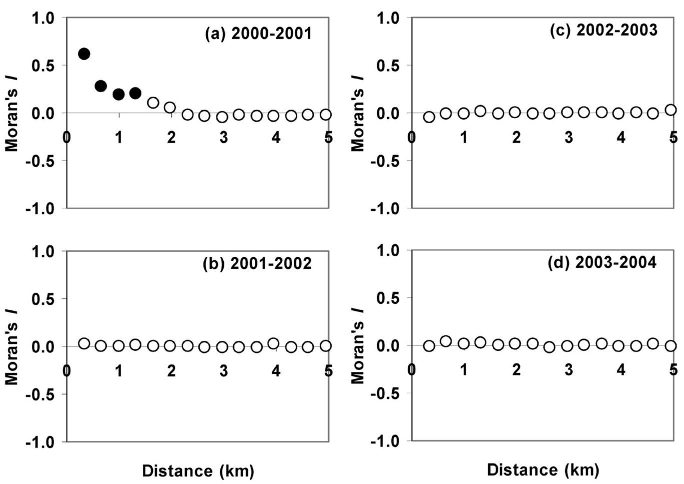

Fig. 3. Spatial structure of *H. coagulata* trap catches as indicated by Moran's *I*. Closed circles indicate significant ($P <$ 0.05) spatial autocorrelation.

Table 1. Mean trap catches of *H. coagulata* in four crop types

Winter season[a]	Citrus			Grape			Stone fruit			Other crops		
	n^b	Mean ± SE	%[c]	n	Mean ± SE	%	n	Mean ± SE	%	n	Mean ± SE	%
2000–2001	361	8.02 ± 1.685	49.0	283	1.80 ± 0.541	11.0	254	3.80 ± 1.224	23.2	26	2.74 ± 1.260	16.7
2001–2002	171	0.10 ± 0.046	19.8	127	0.06 ± 0.019	12.8	115	0.19 ± 0.135	38.2	11	0.15 ± 0.038	29.1
2002–2003	171	0.01 ± 0.002	25.3	127	0.01 ± 0.002	25.1	115	0.01 ± 0.003	25.1	11	0.01 ± 0.007	24.4
2003–2004	171	<0.01 ± 0.001	8.2	127	<0.01 ± 0.001	11.3	115	<0.01 ± 0.002	24.8	11	0.01 ± 0.008	55.7

[a] From November through February.
[b] Total number of trap locations.
[c] Percentage of mean trap catches from each crop type.

2001), we also investigated the effect of the distance from citrus on trap catches by quantifying average trap catches within a specified distance from the citrus groves (i.e., buffer). The buffer size ranged from 0 m (trap catches within citrus) to 1,800 m (the maximum buffer size) by 100-m increments. Buffer analysis was conducted with Spatial Analyst.

Results

H. coagulata individuals were caught consistently throughout the winter. *H. coagulata* trap catches were relatively low in November and formed a peak between late December and early January (Fig. 2), indicating active flight behavior at these times. In the 2000–2001 winter, the overall mean ± SE trap catches of *H. coagulata* were high (4.8 ± 1.21 per trap per wk). *H. coagulata* flight activity was positively autocorrelated (Fig. 3a), indicating two trap counts tended to be similar within ≈1.3 km and independent at >1.7 km. Approximately 72% of *H. coagulata* were caught in citrus and stone fruit (Table 1), and most stone fruit orchards were located near citrus groves (Fig. 1). Although *H. coagulata* were consistently caught in vineyards, trap counts were relatively low compared with other commodity types (Table 2). Mean *H. coagulata* trap catches decreased as the distance from citrus increased (Fig. 4a), indicating that *H. coagulata* catches were higher on traps nearer citrus. This implies that citrus was the main crop where high *H. coagulata* flight activity occurred and *H. coagulata* dispersed from citrus to nearby commodities. We also determined the effect of the distance from citrus on trap catches in stone fruit and grapes. The data showed that trap catches in stone fruit and grape were highest near citrus and decreased as the distance from citrus increased (Fig. 5), further indicating the importance of citrus to *H. coagulata* flight activity in the winter.

Table 2. Trap catches of *H. coagulata* caught in each commodity type in 2000–2001 before the chemical spray program began

Commodity type	Commodity	No. *H. coagulata*/trap/wk ± SE
Citrus	Grapefruit	0.50 ± 0.088
	Lemon	1.86 ± 0.957
	Orange	7.82 ± 0.501
	Tangerine	42.32 ± 6.187
Grape	Raisin grape	0.04 ± 0.011
	Table grape	2.06 ± 0.179
	Wine grape	0.43 ± 0.112
Stone fruit	Almond	0.60 ± 0.058
	Apricot	9.44 ± 4.491
	Cherry	9.60 ± 1.196
	Nectarine	4.40 ± 0.660
	Peach	3.36 ± 0.675
Other crops	Blueberry	1.36 ± 0.236
	Eucalyptus	4.80 ± 0.817
	Fig	0.46 ± 0.243
	Orangeberry	0.80 ± 0.258
	Pistachio	0.51 ± 0.057
	Pomegranate	0.09 ± 0.091

In late February 2001, a chemical control program was initiated by the United States Department of Agriculture, followed by a parasitoid release program conducted by the California Department of Food and Agriculture (CDFA 2005). The control programs targeted *H. coagulata* in citrus because of its importance as an overwintering and reproductive host (Blua et al. 1999, 2001). Fifteen of the 32 citrus blocks in the study areas that reached a mean of one adult *H. coagulata* per tree were treated. Treatments started with foliar applications to ≈607 ha of citrus by using Evergreen (a mixture of pyrethrins and piperonyl butoxide, McLaughlin Gormley King Company, Minneapolis, MN) at 1.68 kg/ha, and to 194 ha with Lannate (methomyl, du Pont de Nemours and Company, Wilmington, DE) at 2.29 kg/ha or Lorsban (chlorpyrifos, Dow AgroSciences, Indianapolis, IN) at 13.5 kg/ha. After the foliar spray, Admire (imidacloprid, Bayer CropScience AG, Monheim, Germany) at 0.56 kg/ha was applied to the soil through the irrigation system in all citrus groves between late March and early April 2001.

These control strategies resulted in mean ± SE trap counts being reduced to 0.041 ± 0.0004 per trap per wk in the following winters. No spatial autocorrelations of trap catches were detected in 2001–2004 (Fig. 3b–d), indicating a random distribution of *H. coagulata* at a scale used in this study. More *H. coagulata* were found in stone fruit than citrus (Table 1), likely because the chemical control programs targeted *H. coagulata* in citrus. After insecticide applications, there was no relationship between *H. coagulata* densities and distance from the citrus as shown in 2000–2001 (Fig. 4b–d). Although trap counts were very low in the 2001–2004 winters, *H. coagulata* were consistently caught in vineyards.

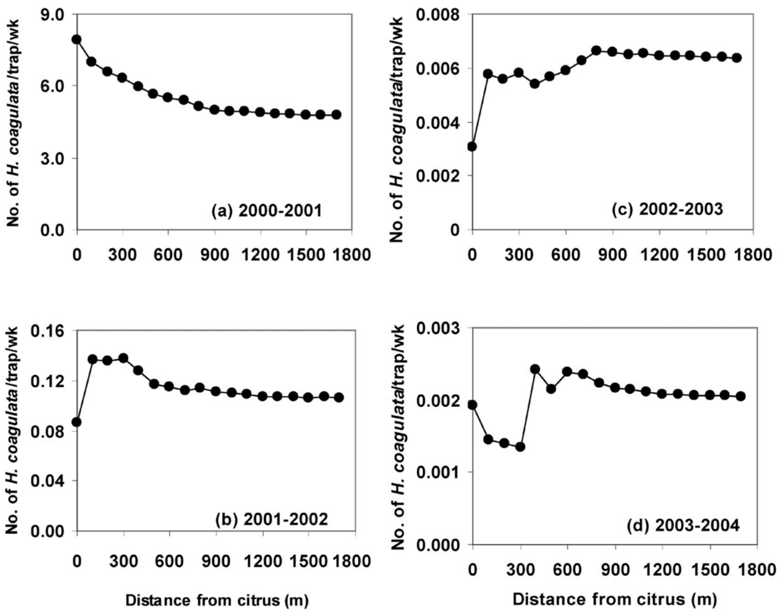

Fig. 4. Effect of distance from citrus on mean *H. coagulata* trap catches.

Discussion

This study shows several significant features of the temporal and spatial distribution of *H. coagulata* during the winter in the lower San Joaquin Valley that likely impact the spread and potential management of PD. First, trap catches indicated *H. coagulata* activity during the winter. Mean trap densities, averaged over all commodities, indicated peak flight activity in late December in all 4 yr of this study. This peak is consistent with *H. coagulata* monitoring in the Coachella Valley, where trap catches of *H. coagulata* exhibited a peak during the winter (Blua et al. 2001, Park et al. 2006a). These peaks of *H. coagulata* activity suggest the potential for the winter-season transmission of *X. fastidiosa.* Weather data from a nearby weather station (≈4 km southwest from the study area) in Arvin (Kern Co.) established by the California Irrigation Management Information System suggested that *H. coagulata* individuals were consistently caught throughout the winter, even though ≈20% of the days had a minimum temperature below 0°C.

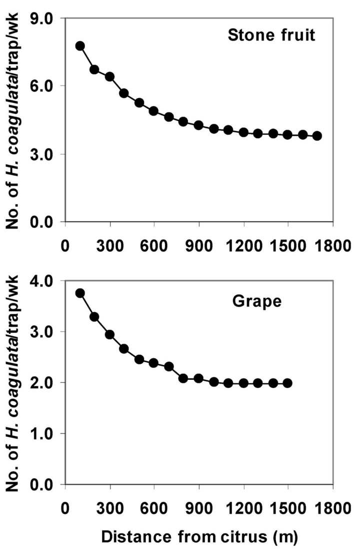

Fig. 5. Effect of distance from citrus on mean *H. coagulata* trap catches in stone fruit and grape in 2000–2001 winter.

Second, sharpshooter numbers on traps in 2000–2001, before an areawide insecticide treatment program was initiated in citrus, were spatially dependent and aggregations were found near citrus. This spatial relationship between citrus and *H. coagulata* also was reported in the Coachella Valley (Park et al. 2006a). Highest densities of *H. coagulata* were on traps in tangerine groves, and 49% of the trap catches were from citrus, whereas the other 51% were from all other commodities combined. Citrus provides a robust vegetative plant for *H. coagulata* at this time of year when there is little other vegetation available, and this feature contributes to its importance in the seasonal survival of *H. coagulata* in this geographic area. Aggregations of *H. coagulata* in citrus during the winter probably influence the movement of *X. fastidiosa* in commodities adjacent to the citrus. Buffer analyses showed that sharpshooter numbers decreased as the distance from citrus increased. Similar results were reported in PD distribution patterns in other areas in California. Perring et al. (2001) documented higher incidence of PD when grapevines were close to citrus in the Temecula Valley, and Park et al. (2006b) found a positive relationship between proximity to citrus and PD incidence in the Coachella Valley.

Third, Almeida and Purcell (2003a) and Almeida et al. (2005) showed that *H. coagulata* can transmit *X. fastidiosa* to mature woody tissues of dormant grapevine and almond during the winter, pointing out the concern for *X. fastidiosa* spread at this time of year. One source of overwintering *H. coagulata* adults in citrus may be those that immigrated from grapevines during the fall. At this time of the year, *X. fastidiosa* titer and distribution within infected vines may be high, because systemic infections in old tissue would have grown during the summer, and new infections had established in new tissue. Given this scenario, a high proportion of the *H. coagulata* immigrating to citrus from an infected vineyard or almond orchard could be carrying *X. fastidiosa.* Active flight of *H. coagulata* in the winter, potentially high numbers of sharpshooters carrying *X. fastidiosa,* impact of citrus proximity to sharpshooter densities in other commodities, and the ability to transmit *X. fastidiosa* to dormant grapes and almonds suggests that winter is an important time of the year in the epidemiological cycle of *X. fastidiosa.*

Revealing these three features can assist in designing temporally and spatially targeted management strategies for *H. coagulata.* For temporally targeted *H. coagulata* management, control measures should be applied to prevent peak densities in late December. Although high numbers of *H. coagulata* have been reported in some areas of the San Joaquin Valley during the winter (CDFA 2005), early winter-season treatments have not been used. There are trade-offs with this strategy, because materials used would be foliar treatments rather than the standard systemic insecticides being used in this area, because citrus is harvested during the winter. Preventing the late December flight peak could reduce the potential winter-season transmission of *X. fastidiosa* in grape and almond. For spatially targeted *H. coagulata* management, specific hosts that harbor *H. coagulata* could be targeted to reduce the first generation of *H. coagulata* in spring (Blua et al. 2001). Our study showed that *H. coagulata* trap catches in all crops were considerably lower after the control program began, even though the chemical control program targeting *H. coagulata* was applied only to citrus. This finding indicates that citrus is the correct commodity for placement of management tactics. In addition to lowering densities throughout the study area, spatial patterns of *H. coagulata* flight activity were altered after the control program began. The lack of spatial dependence after application clearly is related to the very low trap numbers.

Because of these low *H. coagulata* numbers that have resulted from areawide spray programs, it is unlikely that epidemiologists will be able to demonstrate statistical relationships between overwintering *H. coagulata* numbers and PD or almond leaf scorch incidence. Therefore, further epidemiological studies in this geographic area must be conducted at finer scales (i.e., field or field-block scales). A key component of this research is to determine the proportion of *X. fastidiosa*-carrying *H. coagulata* collected during the winter from various commodities.

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